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A camera trapping survey of mammals in the mixed landscape of Bolivia's Chiquitano region with a special focus on the Jaguar

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Abstract
At a site in the Bolivian Chiquitano region composed by a mosaic of pastureland and primary Chiquitano Dry Forest (CDF) we conducted a camera-trapping study to (1) survey the mammals, and (2) compare individual Jaguar numbers with other Chiquitano sites. Therefore, we installed 13 camera stations (450 ha polygon) over a period of six months. On 1,762 camera-days and in 1,654 independent capture events, we recorded 24 mammalian species that represent the native fauna of large and medium-sized mammals including apex-predators (Puma, Jaguar), meso-carnivores (Ocelot, Jaguarundi, Margay), and large herbivores (Tapir, Collared and White lipped Peccary). We identified six adult Jaguars and found indications of successful reproductive activity. Captures of Jaguars were higher in CDF than in altered habitats. In summary, we believe that (1) the mammal species richness, (2) the high capture numbers of indicator species, and (3) the high capture numbers of Jaguar indicate that our study area has a good conservation status. Future efforts should be undertaken to keep this, and monitoring programs in this region are necessary to further evaluate the potential importance of the Chiquitano region as a possible key region for mammals, especially Jaguars, in South America.

Keywords
Camera trapping, Chiquitano Dry Forest, individual identification, *Panthera onca*, species inventory.

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Introduction

Bolivia is a country with high geobiodiversity composed of 12 well-defined ecoregions with several sub-ecoregions ranging from lowlands near sea level to high altitudes of the Andes (Barthlott and Winiger 1998; Ibisch and Mérida 2004). However, the pressure on Bolivian wildlife has increased rapidly during the last decades and has led to irreversible damage (Anderson 1997; Barthlott and Winiger 1998; Brooks et al. 2002; Ibisch and Mérida 2004; Kosydar et al. 2014; Peñaranda and Simonetti 2015; Romero-Muñoz et al. 2019a). Similar to the global situation, human population expansion, deforestation for agriculture and pastureland, destruction and fragmentation of habitats, and hunting are the major threats to Bolivia's rich biodiversity (Ibisch and Mérida 2004; MMAyA 2009; Romero-Muñoz et al. 2019a).

An example of a rapidly changing landscape is the Chiquitano region in eastern Bolivia, where agriculture and cattle ranching are the major forms of land-use and have been the major driver of deforestation in Bolivia during the last decades (Ibisch and Cuéllar 2004; Müller et al. 2012, 2014a, 2014b). The Chiquitano region, located on the Precambrian Shield in the eastern part of the country, is a climatic transition zone between humid and dry forests, and at the same time a forest-savanna ecotone between Amazon, Cerrado and Gran Chaco (Whitmore and Prance 1987; Ibisch and Mérida 2004; Killeen et al. 2006; Navarro 2011; Vides-Almonacid and Justiniano 2011).

The region is rather understudied, but diverse in habitats, fauna and flora alike (e.g. Killeen et al. 2006; Schulze et al. 2009; Jansen et al. 2011; Navarro 2011). Mammal diversity in Bolivia has increased from 321 native species included in Anderson's (1997) seminal work to 406 in the most recent country-wide review (Aguirre et al. 2019). Mammal richness of the Chiquitano region was estimated at 72 species based on museum collections (Brooks et al. 2002), but more recent collections and surveys may increase this total to 133, or more, species in the Museo Noel Kempff Mercado database (CGB 2020) depending on the limits chosen for the region and whether borderline species, typical of Amazonian, Chaco or Pantanal habitats, are counted. Of the 133 species of the CGB records, some 80 of them (~ 60 %) represent bats, small rodents and small marsupials which are largely poorly known and need to be captured for identification. The rest of the Chiquitano species are large and medium-sized mammals that can be surveyed mostly without captures, and 53 of them have been recorded within Chiquitano forest and Cerrado habitats (CGB 2020). Using another source (Wallace et al. 2012), this number increases to 65 species by adding the transition to the Chaco and Pantanal savannas, and to 74 if Amazonian species from the flooded riverine forests in the northern Chiquitano limit are included. The potential diversity of carnivores in this region is very high, and surveys by camera trapping have recorded multiple sympatric felids, rare canids, and several Jaguar (*Panthera onca* (Linnaeus, 1758)) individuals in remnant forests reserves and certified forestry areas of the Chiquitano forest (Arispe et al. 2007b; Polisar et al. 2016). However, large carnivores, and especially Jaguar, listed as Vulnerable in the national Red List (Aguirre and Tarifa 2009), are subject to all above mentioned threats such as habitat destruction, prey depletion and hunting (Wolf and Ripple 2017; Tucker et al. 2018; Jędrzejewski et al. 2018; Romero-Muñoz et al. 2019b).

Monitoring local mammal populations is important because changes in large carnivore or herbivore populations can have severe impacts on currently intact ecosystems. For example, predators play a vital role in structuring and maintaining ecosystems, not only through direct impact on prey species, but further via different functional responses on other herbivores, meso-carnivores and lower trophic levels along several paths within the food web (Ripple et. al. 2014; Soria-Díaz et al. 2018). As a step towards monitoring local mammal diversity and assessing the value of remnant forest for the conservation of Jaguars, we conducted a survey of medium-sized to large mammals in a cattle ranch and private reserve which are representative of the Chiquitano forest. Thus, our objectives were to (1) survey local mammal fauna in various habitats using camera traps; and (2) estimate the number of individual Jaguars in the study area for the comparison with similarly sampled neighbouring Chiquitano sites.

Methods

Study site. Camera trap data were collected on the San Sebastián cattle ranch (16.3622°S, 062.0023°W, 500 m a.s.l.), in the Province of Ñuflo de Chávez, Santa Cruz Department, 18 km south of the town of Concepción, Bolivia. The ranch is at the center of the endemic Chiquitano Dry Forest (CDF), the largest expanse of seasonally dry tropical forests in South America (Miles et al. 2006; Power et al. 2016). The CDF varies from a subhumid semideciduous forest developed on deep, well-drained soils covering most of the Concepción area, to strips of more humid hydrophytic and riverine forests along valleys and streams (Navarro 2011). On shallow soils, limited by a hardpan and scarce nutrients, the tall forest is replaced by a lower stature sclerophyllous woodland or fire-adapted tree savanna typical of the Cerrado (a more detailed description of the area is given by Schulze et al. 2009). Of the total area of the San Sebastián cattle ranch (3,264.9 ha), half is used for farming (pastureland 787.3 ha, 24.1%; forest occasionally used for browsing cattle 727.2 ha, 22.3%), and the other half is a private reserve of low-disturbance, primary Chiquitano Dry Forest (1,673.7 ha; 51.3%). During the study period, 480 heads of cattle were held in the area.

Camera trapping. Between March 2017 and October 2017, 26 infrared cameras (Bushnell Trophy Camera Brown Model 119437) were placed across an area of approximately 450 ha (polygon of cameras). Thirteen camera stations were set, grouped in three areas of different habitat types: (1) secondary forest patch in pastureland: Churrasquera; (2) primary forest: Reserve; and (3) border of pastureland to forest: Puerta Principal (Table 1). Camera stations were opportunistically set along dirt roads, stream beds and game trails to maximize the probability of detecting species. A maximum spacing of roughly 3 km between camera stations was chosen to ensure that home ranges of Jaguar, the focal species, could not fit within gaps between stations. The minimum distance between two camera stations was about 50 m (Fig. 1).

Camera traps were programmed to record 24 h/d and were attached to suitable trees at a height of approximately 40 cm. At each camera station, two cameras were placed opposite to each other in order to record both sides

Table 1. Camera stations, habitat type, and geogrpahic coordinates.

Station_ID	Location	Habitat type	Latitude (°S)	Longitude (°W)
1	Churrasquera	Secondary forest patch in pastureland	16.3688	062.0041
2	Churrasquera	Secondary forest patch in pastureland	16.3695	062.0052
3	Churrasquera	Secondary forest patch in pastureland	16.3703	062.0058
4	Churrasquera	Secondary forest patch in pastureland	16.3701	062.0061
5	Reserve	Primary forest	16.3780	062.0333
6	Reserve	Primary forest	16.3780	062.0353
7	Reserve	Primary forest	16.3782	062.0351
8	Reserve	Primary forest	16.3697	062.0311
9	Reserve	Primary forest	16.3644	062.0280
10	Reserve	Primary forest	16.3623	062.0220
11	Puerta Principal	Border of pastureland to forest	16.3448	062.0093
12	Puerta Principal	Border of pastureland to forest	16.3449	062.0093
13	Churrasquera	Secondary forest patch in pastureland	16.3707	062.0059

of individually identifiable animals. One camera was set to take images with a minimum delay of 5 sec and with a burst of three images per trigger event. Because preliminary studies with that camera type had resulted in often fuzzy night shots, but clearer images of individual coat pattern of Jaguars on videos, the second camera was set to video mode, recording for 15 sec and with a minimum delay of 5 sec, to increase the probability of capture of individual coat pattern of Jaguar. Each camera trap was visited approximately every two weeks to change batteries and download images from the SD cards. From photographs and videos, detected mammals were identified to species level when possible, according to diagnostic traits and previous studies in the region (Anderson 1997; Wallace et al. 2010). Taxonomy followed the last review of the Bolivian mammals (Aguirre et al. 2019). Individual Jaguars were further identified by their unique coat patterns of rosettes to estimate the minimum number of individuals and their occurrence in within the study area. Age (subadult or adult) and sex were assigned according to the individual Jaguar's size and the appearance of external genitalia, respectively.

Statistical analysis. Camera trap data were analysed following the workflow suggested in the open-source R package *camtrapR* (Niedballa et al. 2016). Images were processed using the open-source software Digicam (version 5.5.0). Images from both cameras at one station were pooled and independent capture events were defined using a minimum time difference of 30 min to avoid double counting and temporal autocorrelation through multiple images of the same individual within a short time frame (Silveira et al. 2003). Species accumulation curves (SAC) were calculated using the vegan package (Oksanen et al. 2017) in order to evaluate the sampling quality and survey effort needed for determining

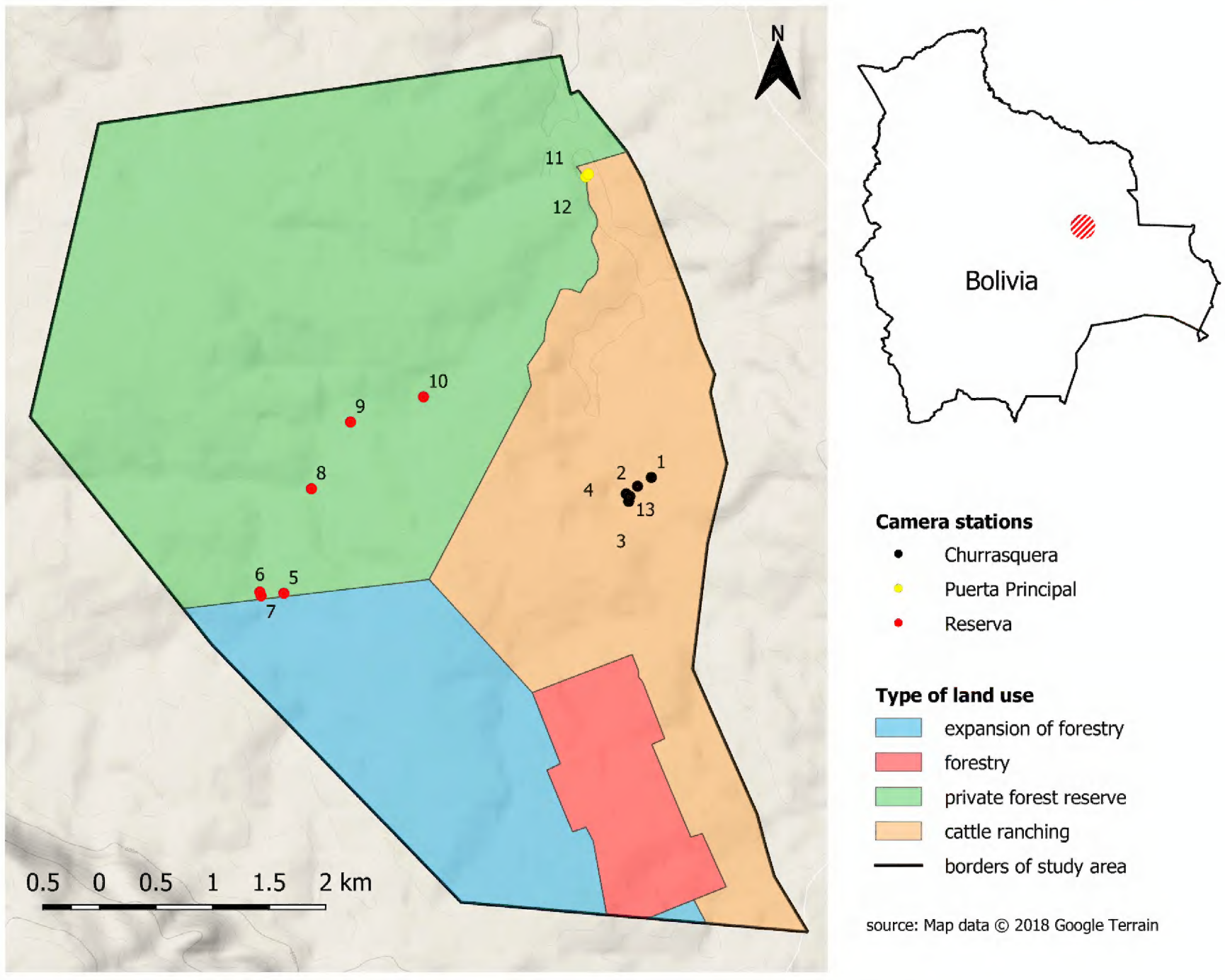

Figure 1. Study area showing land use types and location and organization of camera stations 1–13.

species richness. "Exact" methods were applied to find the expected species accumulation curve by using sample-based rarefaction as described in Ugland et al. (2003) and Colwell et al. (2004). Observations of domestic animals such as dogs and cattle, as well as non-mammalian species, were omitted from the analysis of mammalian species richness.

Non-parametric statistics (Wilcoxon Mann-Whitney *U* test) were used to compare individual Jaguar counts and species richness between intact primary forest (n = 4) and pastureland including its borders to the forest (n = 6), after incorporating only cameras with at least 70 active trapping days to ensure reasonable enough survey time at each station. All statistical analyses were conducted using the statistical open-source environment R v. 3.4.1 (R Development Core Team 2016).

Results

Species richness. Over the entire survey period of 198 days, we recorded 40,000 images and videos, resulting in 1,654 independent capture events of vertebrates detected during 1,762 independent camera trapping days. Cameras recorded 1,279 independent captures of 24 wild mammalian species and 155 captures of domestic animals such as cattle and dogs (Table 2) as well as 211 records of 17 bird species, and nine captures of two reptile species (Table 3). From these, there were 246 independent captures of apex-predators such as Jaguar and Puma (*Puma concolor* (Linnaeus, 1771)) and mesocarnivores, e.g. Crab-eating Fox (*Cerdocyon thous* (Linnaeus 1766)), Jaguarundi (*Herpailurus yagouaroundi* (É. Geoffroy Saint-Hilaire, 1803)) and Ocelot (*Leopardus pardalis* (Linnaeus, 1758)). Three Near Threatened species were detected: Jaguar, Margay (*Leopardus wiedii* (Schinz, 1821)) and Neotropical Otter (*Lontra longicaudis* (Olfers, 1818)) (IUCN 2019). Moreover, South American Tapir (*Tapirus terrestris*) and White-lipped Peccary (*Tayassu pecari* Fischer, 1814) occurred within the study area; both are Vulnerable (IUCN 2019). On the national Red List (MMAyA 2009), Jaguar and Tapir are in Vulnerable, and Neotropical Otter, Margay, White-lipped Peccary, and Collared Peccary (*Pecari tajacu* (Linnaeus, 1758)) are Near Threatened. Selected identification traits and distribution data of the recorded species according to Wallace et al. (2010) are included below.

The cumulative number of detected mammal species followed an expected asymptotic trend (Fig. 2). The species accumulation curves (SAC) showed a rapid increase within the first 200 camera days before levelling off

Table 2. Mammal species detected via camera trapping, their IUCN Red List category (IUCN 2019) and the total number of independent capture events. Red List categories: DD = Data Deficient; LC = Least Concern; NT = Near Threatened; VU = Vulnerable.

Taxon	Common name	IUCN status	Libro Rojo Bolivia (2009)	Independent captures
Marsupialia				
Order Didelphimorphia				
Family Didelphidae				
aff. *Marmosa* sp.	Mouse opossum sp.	LC		4
Didelphis marsupialis	Black-eared Opossum	LC		25
Eutheria				
Superorder Xenarthra				
Order Pilosa				
Family Myrmecophagidae				
Tamandua tetradactyla	Southern Tamandua	LC		8
Order Cingulata				
Family Dasypodidae				
Dasypus novemcinctus	Nine-banded Armadillo	LC		77
Boreotheria				
Order Cetartiodactyla				
Family Cervidae				
Mazama gouazoubira	Gray Brocket Deer	DD	LC	88
Family Tayassuidae				
Pecari tajacu	Collared Peccary	LC	NT	235
Tayassu pecari	White-lipped Peccary	VU	NT	23
Order Primates				
Family Cebidae				
Sapajus apella	Tufted Capuchin	LC		6
Order Carnivora				
Family Canidae				
Cerdocyon thous	Crab-eating Fox	LC		34
Family Felidae				
Herpailurus yagouaroundi	Jaguarundi	LC	DD	7
Leopardus pardalis	Ocelot	LC	LC	30
Leopardus wiedii	Margay	NT	NT	4
Puma concolor	Puma	LC	LC	13
Panthera onca	Jaguar	NT	VU	137
Family Mustelidae				
Lontra longicaudis	Neotropical Otter	NT	NT	3
Eira barbara	Tayra	LC		21
Family Procyonidae				
Nasua nasua	South American Coati	LC		39
Order Lagomorpha				
Family Leporidae				
Sylvilagus brasiliensis	Forest Rabbit	LC		58
Order Rodentia				
Family Caviidae				
Hydrochoerus hydrochaeris	Capybara	LC		1
Family Dasyproctidae				
Dasyprocta azarae	Azara's agouti	LC		336
Family Cuniculidae				
Cuniculus paca	Lowland Paca	LC		39
Family Sciuridae				
Hadrosciurus spadiceus	Bolivian Squirrel	DD		72
Family Erethizontidae				
Coendou prehensilis	Brazilian Porcupine	LC		1
Order Perissodactyla				
Family Tapiridae				
Tapirus terrestris	South American Tapir	VU	VU	19
Domestic animals				
Bos taurus	Cattle	—		154
Canis lupus familiaris	Domestic dog	—		1
Unidentified	—	—		35
Total				**1690**

Table 3. Other species detected via camera trapping, their IUCN Red List category (IUCN 2019) and the total number of independent capture events.

Taxon	Common name	IUCN status	Libro Rojo Bolivia (2009)	Independent captures
Class Aves				
Aramides ypecaha	Giant Wood-rail	LC		4
Aramus guarauna	Limpkin	LC		2
Ardea cocoi	Cocoi Heron	LC		1
Cariama cristata	Red-legged Seriema	LC		30
Cathartes burrovianus	Lesser Yellow-headed Vulture	LC		6
Cochlearius cochlearius	Boat-billed Heron	LC		3
Columba speciosa	Scaled Pigeon	LC		1
Coragyps atratus	Black Vulture	LC		2
Crax fasciolata	Bare-faced Curassow	VU		76
Crypturellus parvirostris	Small-billed Tinamou	LC		2
Crypturellus tataupa	Tataupa Tinamou	LC		4
Crypturellus undulatus	Undulated Tinamou	LC		18
Cyanocorax chrysops	Plush-crested Jay	LC		4
Eurypyga helias	Sunbittern	LC		3
Leptotila verreauxi	White-tipped Dove	LC		34
Momotus momota	Amazonian Motmot	LC		6
Penelope superciliaris	Rusty-margined Guan	LC		1
Pilherodius pileatus	Capped Heron	LC		2
Pyrrhura molinae	Green-cheeked Parakeet	LC		1
Tigrisoma lineatum	Rufescent Tiger-heron	LC		1
Unidentified		—		24
Class Reptilia				
Salvator merianae	Argentine Black and White Tegu	LC		8
Chelonoidis carbonarius	Red-footed Tortoise	VU	NT	1

shortly after, with 90% (21.6 species ± 1.1 SD) of all species being detected just after 549 camera days. Some species, e.g. the arboreal opossum (aff. *Marmosa* sp.) and the Neotropical Otter required a considerably longer survey time before being detected (1,067 and 1,251 effective camera trapping days, respectively).

The comparison of species richness between different habitats revealed no significant difference between forest (median = 12) and pasture land (median = 11; Wilcoxon Mann-Whitney U test, $U = 14.5$, $p = 0.66$).

Annotated list

Order Didelphimorphia
Family Didelphidae

aff. *Marmosa* sp. Gray 1821

Mouse opossum sp., Carachupa
Figure 3

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; 16.3707°S, 062.0059°W; camera station 12 (Table 1); first capture on 18 July 2017; secondary forest patch in pastureland.

Identification. This small, arboreal opossum was identified to genus by its size and slender body. However, without a specimen it is impossible to identify the species, and even the diagnosis of the genus is difficult. Thus, this opossum belonging to the genera *Gracilinanus* Gardner & Creighton, 1989 or *Marmosops* Matschie, 1916 is possible as well.

Didelphis marsupialis Linnaeus, 1758

Black-eared Opossum, Zarigüeya común
Figure 4A

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 1, 3, 4, 5, 6, 7, 8, 11, 13 (Table 1); first capture on 29 March 2017; secondary forest patch in

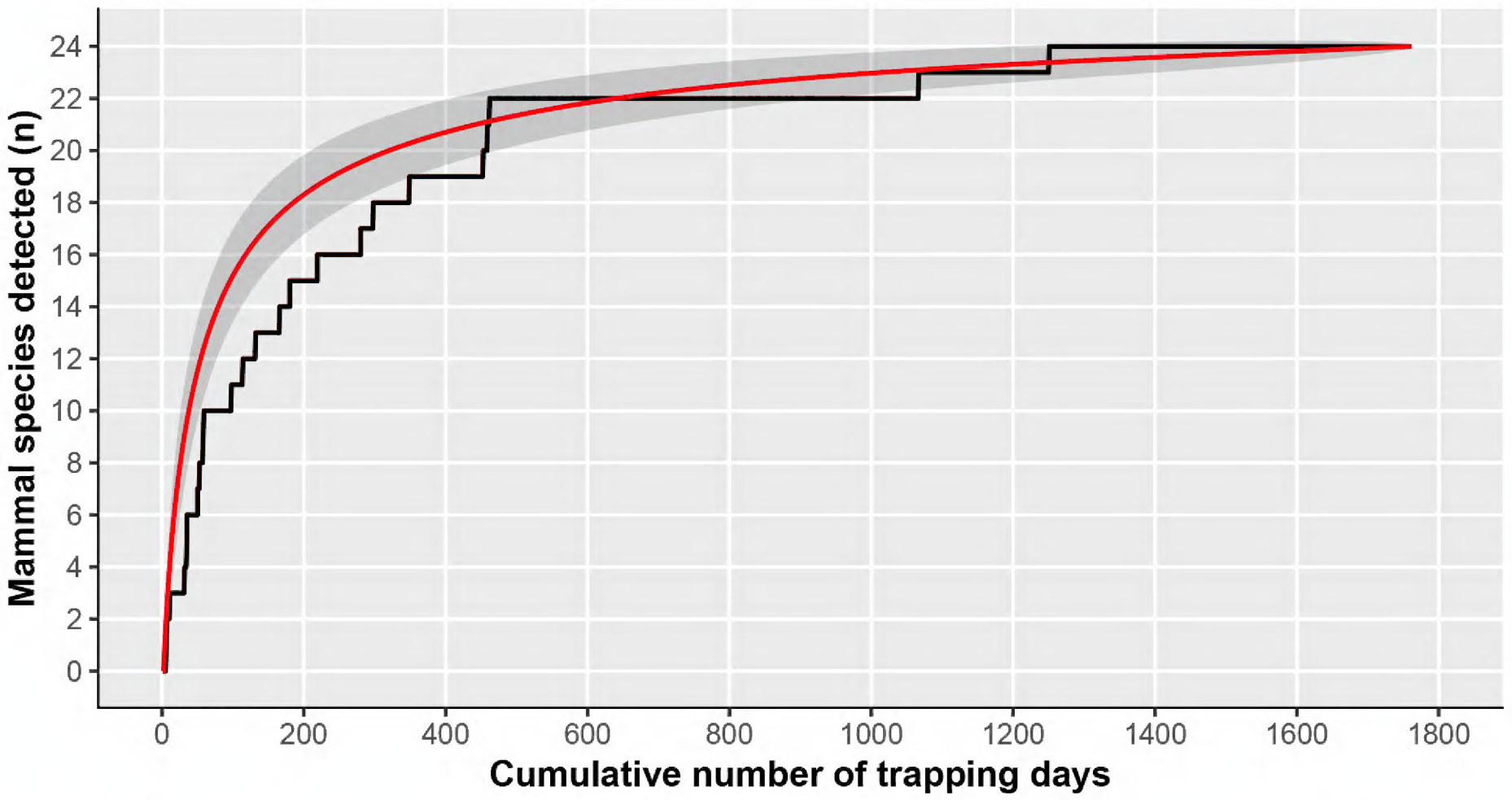

Figure 2. Modeled species accumulation curves (SAC, red) with 95% confidence interval (shaded area) and number of mammal species (black line) detected over the study period from 13 camera stations.

Figure 3. Possible Mouse opossum sp. (aff. *Marmosa* sp.) detected at Hacienda San Sebastián through a camera trapping survey carried out from March to October 2017.

pastureland, primary forest, and border of pastureland to forest.

Identification. *Didelphis marsupialis* is a medium-sized opossum that has large, black ears, pale fingers, and a face and tail without hair. The similar *D. albiventris* Lund, 1840 has a white face and white ears and is not known from the region.

Order Pilosa
Family Myrmecophagidae

***Tamandua tetradactyla* (Linnaeus, 1758)**
Southern Tamandua, Oso hormiguero
Figure 4B

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera trap stations 3, 8, 9 (Table 1); first capture on 24 April 2017; secondary forest patch in pastureland and primary forest.

Identification. This is a medium-sized anteater species with elongated snout, a prehensile tail, and short, yellowish fur covered by a black vest on the back and two black scapular stripes on the chest.

Order Cingulata
Family Dasypodidae

***Dasypus novemcinctus* Linnaeus, 1758**
Nine-banded Armadillo, Tatú mula
Figure 4C

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 1, 3, 4, 8, 9, 10, 11, 12 (Table 1); first capture on 23 March 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. This is a medium-sized to large armadillo (2–6 kg) with a carapace that covers the body and nine mobile bands in the median region of the body. The long is tail with rings of scales. It is a common and widespread armadillo species, and is similar in shape to the much rarer *Dasypsus septemcinctus* Linnaeus, 1758 and *D. kappleri* Kraus, 1862 which show fewer mobile bands and have not been recorded in the region of our study area.

Order Cetartiodactyla
Family Cervidae

***Mazama gouazoubira* (Fischer, 1814)**
Gray Brocket Deer, Urina
Figure 4D

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; 1, 3, 4, 5, 8, 9, 10, 11, 12 (Table 1); first capture on 23 March 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. This is the most common cervid in the dry forests of lowland Bolivia. Its overall color is grayish brown with the mid-back and outer side of legs a little darker and the throat, neck and venter grayish and lighter. It is smaller than Red Brocket Deer, *Mazama americana* (Erzleben, 1777) (13–23 kg vs 17–30 kg), which shows a reddish-brown coat overall with a contrasting whitish throat. Red Brockets do occur in the region but are rarer (Rivero et al. 2005), limited to taller forest, and were not recorded in this survey.

Family Tayassuidae

***Pecari tajacu* (Linnaeus, 1758)**
Collared Peccary, Taitetú
Figure 4E

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 1, 2, 3, 4, 5, 8, 9, 10, 11, 12 (Table 1); first capture on 29 March 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. This is a grayish, native pig with a white collar around its neck. It is smaller in size (15–30 kg) to Peccary, *Tayassu pecari*, and forms smaller groups of 4–17 individuals.

***Tayassu pecari* Fischer, 1814**
White-lipped Peccary, Tropero
Figure 4F

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 2, 10, 11, 12 (Table 1); first capture on 18 April 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. This is a black or dark brown wild pig that has white markings along the lower part of the snout and no white collar. It is larger (25–37 kg) than Collared Peccary and forms groups of 50–300 individuals.

Order Primates
Family Cebidae

***Sapajus apella* (Linnaeus, 1758)**
Tufted Capuchin, Mono martin
Figure 4G

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 2, 3, 6, 12 (Table 1); first capture on 14 April 2017; secondary forest patch in pastureland,

Figure 4. Mammal species detected at Hacienda San Sebastián through a camera trapping survey carried out from March to October 2017. **A.** *Didelphis marsupialis*, **B.** *Tamandua tetradactyla*, **C.** *Dasypus novemcinctus*, **D.** *Mazama gouazoubira*, **E.** *Tayassu pecari*, **F.** *Pecari tajacu*, **G.** *Sapajus apella*, **H.** *Cerdocyon thous*, **I.** *Herpailurus yagouaroundi*, **J.** *Leopardus pardalis*, **K.** *Leopardus wiedii*, **L.** *Puma concolor*, **M.** *Panthera onca*, **N.** *Lontra longicaudis*, **O.** *Eira barbara*, **P.** *Nasua nasua*, **Q.** *Sylvilagus brasiliensis*, **R.** *Hydrochoerus hydrochaeris*, **S.** *Dasyprocta azarae*, **T.** *Cuniculus paca*, **U.** *Hadrosciurus spadiceus*, **V.** *Tapirus terrestris*.

primary forest, and border of pastureland to forest.

Identification. This is a medium-sized but robust (2–4.5 kg) primate, which is widespread through most of Boliva, although there are uncertain taxonomic differences and range limits with other robust capuchins. It has a rough, brown fur overall, with darker arms, legs and tail, and a black cap or two black hair tufts on the crown.

Order Carnivora

Family Canidae

***Cerdocyon thous* (Linnaeus 1766)**
Crab-eating Fox, Zorro de monte
Figure 4H

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 1, 3, 6, 9, 10, 12 (Table 1); first capture on 27 March 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. This is the most common native canid in the region and is identified by its medium-sized (3.5–7 kg), robust body, which has a dense coat of grayish to brownish fur. The legs are black and there is a darker stripe along the back and along the tail. The other fox in the region is the Pampas Fox, *Lycalopex gymnocercus* (Waldheim, 1814), which has yellow legs and was not found at this site.

Family Felidae

Herpailurus yagouaroundi (É. Geoffroy Saint-Hilaire, 1803)
Jaguarundi, Yaguarundi
Figure 4I

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 3, 4, 6, 8, 9 (Table 1); first capture on 30 March 2017; secondary forest patch in pastureland and primary forest.

Identification. Five feline species were identified based on body size and coat patterns. *Herpailurus yagouaroundi* was identified by its unique long body and tail and uniform brown coloration.

***Leopardus pardalis* (Linnaeus, 1758)**
Ocelot, Gato de monte
Figure 4J

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 1, 2, 3, 4, 6, 7, 8, 11, 12, 13 (Table 1); first capture on 27 March 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. This species was identified by its relative large body size (7–12 kg), its pattern of coalescing rosettes forming oblique lines on the sides of the body, and its relatively short tail in comparison to other *Leopardus* species.

***Leopardus wiedii* (Schinz, 1821)**
Margay, Tigrecillo
Figure 4K

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 1, 4, 9, 10, 11 (Table 1); first capture on 13 June 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. *Leopardus wiedii* is a spotted cat; it is smaller than ocelot (3–8 kg) and has similarly aligned rosettes, but not quite fused together, a relatively longer tail, larger eyes, and protruding snout.

***Puma concolor* (Linnaeus, 1771)**
Puma, Puma o León
Figure 4L

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 8, 9, 10 (Table 1); first capture on 8 April 2017; primary forest.

Identification. This is a large felid (30–60 kg), with a long body, small head, round ears, and a long tail. The coat is uniformly light brown to reddish.

***Panthera onca* (Linnaeus, 1758)**
Jaguar, Jaguar ó Tigre
Figure 4M

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 12, 13 (Table 1); first capture on 26 March 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. Body size, shape, and coat pattern are unmistakable.

Family Mustelidae

***Lontra longicaudis* (Olfers, 1818)**
Neotropical Otter, Lobito de río
Figure 4N

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; 16.3780°S, 062.0353°W; first capture on 8 August 2017; primary forest.

Identification. This river otter has dark brown-gray fur, which is lighter around the throat and snout, short legs, and long and rather stout tail. It is solitary and much smaller (5–10 kg) than the social Giant River Otter (*Pteronura brasiliensis* (Zimmermann, 1780)) found in larger rivers farther north and east of our study area.

***Eira barbara* (Linnaeus, 1758)**
Tayra, Melero
Figure 4O

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 1, 2, 3, 4, 6, 7, 8, 11, 12, 13 (Table 1); first capture on 1 May 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. The melero or Tayra is a medium-sized mustelid (3–7 kg), with a long body and neck, short limbs, and a long, hairy tail. The body is dark brown, except for the head and neck, which is lighter brown, and the throat, which has a whitish spot.

Family Procyonidae

***Nasua nasua* (Linnaeus, 1766)**

South American Coati, Tejón
Figure 4P

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 1, 2, 3, 4, 6, 7, 8, 11, 12, 13 (Table 1); first capture on 6 April 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. This is a medium-sized procyonid (2–5 kg), with a triangular head, long and pointed snout, short ears and a long, black-striped tail. The body coloration varies from orange to light or dark brown.

Order Lagomorpha
Family Leporidae

***Sylvilagus brasiliensis* Linnaeus, 1758**
Forest Rabbit, Tapití
Figure 4Q

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 3, 4, 5, 6, 9, 10, 11 (Table 1); first capture on 30 March 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. This is a small forest rabbit (0.5–1.2 kg) with relatively long ears (but shorter than other lagomorphs), an agouti-brown body, and a black tail.

Order Rodentia
Family Caviidae

***Hydrochoerus hydrochaeris* (Linnaeus, 1766)**
Capybara, Capiguara
Figure 4R

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; 16.3697°S, 062.0311°W; first capture on 12 May 2017; primary forest.

Identification. This species, the largest rodent in the world, is unmistakable due to the shape of the head, short ears, and uniformly colored body, which varies from reddish to grayish brown.

Family Dasyproctidae

***Dasyprocta azarae* (Lichtenstein, 1823)**
Azara's Agouti, Jochi colorado
Figure 4S

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 1, 2, 3, 4, 5, 8, 9, 10, 11, 12, 13 (Table 1); first capture on 23 March 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. This is a medium-sized rodent (2–4 kg) and is typically grizzled brown, yellowish and black, or grizzled black and orange. The back is rounded and the legs long and skinny. Its taxonomy is not well resolved, but *D. azarae* should be the only agouti species south of the Beni River in Bolivia.

Family Cuniculidae

***Cuniculus paca* (Linnaeus, 1766)**
Lowland Paca, Jochi pintado
Figure 4T

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 3, 6, 11, 12 (Table 1); first capture on 4 April 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. This is a robust, medium-sized to large (6-10 kg), nocturnal rodent. The body is covered by short, brown fur with longitudinal rows of white spots.

Family Sciuridae

***Hadrosciurus spadiceus* (Olfers, 1818)**
Bolivian Squirrel, Masi
Figure 4U

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 3, 8, 10, 12 (Table 1); first capture on 12 April 2017; secondary forest patch in pastureland, primary forest, and border of pastureland to forest.

Identification. This is a large-bodied species of squirrel with a typically reddish-brown body having whitish underparts and a thick, brown and orange tail. The similar *Notosciurus pucheranii* (Fitzinger, 1867) is grayish and has a white, subcircular eye-ring.

Family Erethizontidae

***Coendou prehensilis* (Linnaeus, 1758)**
Brazilian Porcupine, Puercoespín

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; 16.3695°S, 062.0052°W; first capture on 12 May 2017; secondary forest patch in pastureland.

Identification. This is a medium-sized, arboreal rodent (2–5 kg). Thick spines, 2–6 cm long, cover the entire body except for the muzzle. The general color appears gray or yellowish from a distance, but each spine is whitish at its base and tip and with a dark-brown band in the middle. This is the only porcupine species known in the area.

Order Perissodactyla
Family Tapiridae

***Tapirus terrestris* (Linnaeus, 1758)**
South American Tapir, Anta ó Tapir
Figure 4V

Examined material. BOLIVIA; Province of Ñuflo de Chávez of Santa Cruz Department; Centro "Chiquitos"; camera stations 9, 10, 11, 12 (Table 1); first capture on 11 May 2017; primary forest and border of pastureland to forest.

Identification. The Tapir is an unmistakable, large mammal with a uniformly dark gray-brown body, a short hair crest along the neck, and a long, flexible nose.

Captures of Jaguar individuals. Of the 137 capture events of Jaguars, at least seven individuals could be identified by their individual coat patterns (Table 4). Six individuals were adult; two were females (#2 and 5), three were males (#1, 3 and 6), and one was undetermined (#4) because sex-specific traits were not apparent in the images. For 15 capture events, the individual could not be explicitly identified, as the quality of images was too low. One adult female was observed with a young, which indicates reproductive success of this species within the study site. We compared the number of capture events of Jaguars with the two types of land use (primary forest vs altered habitat) in the study area to test the hypothesis that there would be more Jaguar detections in primary forest than in altered habitat. Camera stations in forests had a higher number of Jaguar occurrences (median = 22) than those in semi-open pastureland (median = 8; Wilcoxon Mann-Whitney U test, $U = 24$, $p = 0.014$).

Discussion

In our study, 24 mammal species were recorded by camera trapping. As the SAC reached a state with little increase in detection of new species over time, we suggest that this number is close to the actual number of mammal species detectable by this study design. We recorded the two top predators of South America, Puma and Jaguar, as well as several meso-carnivores, large herbivores such as Tapir and two species of Peccaries, and several other small to medium-sized mammals. Two species are Vulnerable, three or four species are Near Threatened according to IUCN or the Red List of Bolivia (IUCN 2019; Tarifa and Aguirre 2009; Table 2). Many favorable game species, such as White-lipped Peccary, Tapir, Brocket Deer, as well as the frugivorous bird, Bare-faced Curassow (*Crax fasciolata*), can decline under hunting pressure (de Thoisy et al. 2010), because they have long generation times and lower fecundity than other species and/or specialized habitat requirements (Peres 2000; Reid 2009). Thus, the high numbers of captures of these species might be a sign for a low hunting pressure in our study area.

To assess the number of species in comparison to other forest sites in the region, we examined results from five camera trapping surveys conducted in the Chiquitano region at sites located between 40 and 330 km away from ours (Table 5). Camera trapping surveys lasting two months at the San Miguelito cattle ranch and private reserve (Rumiz et al. 2003; Arispe et al. 2005) found 30 species of mammals, recording more xenarthrans (notably the giant armadillo *Priodontes maximus*), two Spiny Rats (Echimyidae), Geoffroy's Cat (*Leopardus geoffroyi*), and Red Brocket Deer, which were not present among the 24 species seen in our study. However, the greater number of species in San Miguelito might be due a higher diversity of habitats, including a large river and flooded areas. A smaller sampling in San Miguelito (Kosydar et al. 2014; not included in Table 5) recorded 23 species but missing the two large cats and one Peccary seen in the previous surveys and in our study. Sampling in nearby Altavista ranch and reserve (Venegas et al. 2010) rendered 27 species, with more xenarthrans and rodents than in our study. Surveys far to the east in two large forestry areas, Angel Sandoval (Venegas et al. 2009) and El Encanto (Arispe et al. 2007a, 2007b) recorded fewer species (23 and 19, respectively) despite their similar effort, but discovered notable species such as Giant Armadillo and Bush Dog (*Speothos venaticus*; see overview of the latter study areas in Polisar et al. 2016).

We found six adult Jaguar individuals and indications of successful reproductive activity within the study area (Table 4). The comparison of Jaguar captures between primary forest and altered habitat revealed a higher number of individuals in intact forest, a pattern similar to other studies (e.g. De Souza et al. 2018). The lower numbers of Jaguar in altered habitat might be due to existence of fences (though still passable) and disturbance by (usually mounted) staff; moreover, natural prey seems to be abundant in the intact forest, which might render foraging in pasture relatively unattractive for Jaguar (Khorozyan et al. 2015). Quantifying and evaluating Jaguar or prey density is beyond the scope of this study, and we suggest that future studies should address this in detail. We observed six Jaguars within a small camera polygon (450 ha), but found a high abundance of Jaguars in comparison to other sites in the region (Kosydar et al. 2014; Polisar et al 2016; Table 5). We cannot exclude that these high densities are a consequence of local pressure such as deforestation or hunting in adjacent areas. Nevertheless, future studies could test if Jaguar density is regularly high in the study area or if the higher abundance is due to migration from connected blocks of remnant forest.

In summary, we believe that our data show that the study area is in a good state of preservation because of the (1) high mammal species richness; (2) high capture numbers (suggesting high abundance) of indicator species, such as Peccary, Tapir, and Currasow; (3) the high number of captures of the Jaguar; and (4) the high

Table 4. Individual Jaguars detected within the study site and their respecting number of capture events (by areas).

ID	Sex	Age	Number of capture events by areas			
			Total	Churrasquera	Reserva	Puerta Principal
#1	Male	Adult	43	2	41	0
#2	Female	Adult	25	23	1	1
#3	Male	Adult	39	2	35	2
#4	Unknown	Adult	1	1	0	0
#5	Female	Adult	12	0	12	0
#6	Male	Adult	1	0	1	0
#7	—	Subadult	1	1	0	0
Unknown*	—	—	15	3	11	1

* Jaguar observations could not be clearly identified because of the poor quality of the photos or videos.

Table 5. Comparison of similar camera trap studies in nearby localities of Chiquitano Dry Forests/Cerrado environments. Data taken from Rumiz et al (2003), Arispe et al. (2005, 2007b), Venegas et al. (2010) and Polisar et al. (2016).

Locality (distance from this study)	*N* CT stations	*N* study days	Polygon size (km²)	*N* Jaguar individuals (male, female, unsexed) & cubs	Total mammal spp. recorded by CT	*N* mammal spp. per group and notable examples
Altavista (40 km NE)	20	64	43	2, no	27	1 opossum; 4 edentates w/ Giant Armadillo; 10 carnivores w/5 felids; Tapir; 2 deers; 2 peccaries; 7 rodents; Tapiti
A. Sandoval (330 km SE)	39	56	125	2, 4, 0, yes	19	5 edentates w/ Giant Armadillo; 7 carnivores w/ 4 felids; Tapir; 2 deers; 3 rodents; Tapití
EL Encanto (250 km E)	20	58	36	4, 0, 0, no	23	2 edentates; 1 monkey; 10 carnivores w/ 6 felids & speothos; 2 deers; Tapir; 1 peccary; 6 rodents
San Miguelito I and II (80 km S)	28	64	24	2, 3, 1, yes	30	1 opossum; 6 edentates w/ Giant Armadillo, 1 monkey; 11 carnivores w/ 6 felids; Tapir, 2 deers, 2 peccaries; 5 rodents; Tapiti
	25	60	54	4, 2, 0, yes	30	1 opossum; 6 edentates w/ giant armadillo; 9 carnivores w/ 5 felids; Tapir; 2 deers; 2 peccaries, 7 rodents; Tapití
San Sebastián (This study)	13	198	4.5	3, 2, 2, yes	24	2 opossums; 2 edentates; 1 monkey; 9 carnivores w/ 5 felids; tapir; 1 deer; 2 peccaries; 5 rodents; Tapití

number of individual Jaguars. In general, the comparisons with other Chiquitano sites suggest that the remnant CDF areas harbour a high diversity of mammals and a good habitat for the Jaguar, probably through a network of natural and subnatural protected areas, forest management operations, and private reserves (Vides-Almonacid and Justiniano 2011).

However, the loss of ecosystem structures primarily through land conversion and wildfires could further result in a decline of biodiversity (e.g. Romero-Muñoz et al. 2019a). It is therefore crucial to increase conservation efforts for the region given the increased human pressure, such as monitoring local populations of Jaguar, which is an umbrella species, flagship species, keystone species, and wilderness quality indicator (e.g. Caro and O'Doberty 1999; Thornton et al. 2016). Moreover, local monitoring programs could help to understand human–Jaguar conflicts that may be enhanced by increased human activities, e.g. hunting and deforestation (Kosydar et al. 2014; De Souza et al. 2018).

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Authors' Contributions

MJ led the study; MJ and ME designed the study; ME and MB tagged photos; ME analyzed the data; MJ, ME, DR and OK wrote the text; JA led the data collection and management; MJ, ME, MB, JA, and DR identified species; ME and MJ made the figures; MJ and OK provided acquisition of external funding.

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